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Rumslig och tidsmässig variation i kvaliteten på herbivorers sommarföda längs en nord-syd-gradient

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Keywords: nutrient variability, *Betula pubescens*, *Epilobium angustifolium*, near infrared reflectance spectroscopy, Sweden, spatiotemporal scales

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Abstract

The spatial and temporal variation in nutritional quality of plants consumed by herbivores is considered as one of the main factors governing their feeding patterns and influencing their productivity. Plant nutrients vary in space and time both within and among plant species, at fine scales, and across large geographical scales, creating a heterogeneous environment where herbivores have to cope with variation in food quality at different spatiotemporal scales. As a response to this variation, herbivores make trade-offs between acquisition of digestible nutrients (e.g. nitrogen) and reduction of digestibility-reducing compounds (e.g. plant defence compounds like phenolics or tannins). Since little is known where the major sources of variation that herbivores face are and how these may be compared in a natural system, I analysed spatial and temporal variation in food quality (i.e. the concentration of nitrogen, fiber, total phenolics and condensed tannins) at three levels: local, regional and yearly scales. Two important plant species, downy birch (*Betula pubescens*) and fireweed (*Epilobium angustifolium*), in the summer diet of moose (*Alces alces*) were collected for three subsequent years along a latitudinal gradient of varying environmental conditions spanning across Sweden and assessed with near infrared reflectance spectroscopy. The degree of variation in nutritional aspects of food quality was of similar importance at all three spatiotemporal scales. In addition, there was a clear latitudinal gradient of these nutrients, where nitrogen and fiber increased towards the south in both species, and defence compounds increased towards the north in fireweed. My findings may have important implications for researchers dealing with multiple sources of variation in large scale questions, like climate change and its effects on plant-herbivore interactions.

Introduction

Evaluation of spatial and temporal variation in food resources has long been recognized as an important factor for better understanding of the dynamics of ecosystem processes (Prins and Van Langevelde 2008; Rougharden 1974, Skidmore and Ferwerda 2008). Indeed, successful reproduction and survival of individuals as well as offspring growth often depend upon the ability of individuals to cope with spatial and temporal heterogeneity in food resources (Giesel 1976, Moen et al. 1997, Parker et al. 2009, Pettorelli et al. 2003, Post et al. 2008). Mammalian herbivores have long been known not to simply consume any plant species they encounter, but to respond to spatial and temporal variation in food quality (i.e. in terms of the content of nutrients, digestible energy and digestible-reducing compounds) by demonstrating preferences for different plant species and individual plant parts higher in some nutritional components and lower in other components (e.g. Belovsky 1981, Palo and Robbins 1991, Stolter et al. 2005). The proportions of individual plant species in the diet often differ from the proportions of plants which are actually available in the environment (Palo and Robbins 1991; White and Trudell 1980). It is therefore not surprising that many studies have revealed that variations in plant nutrients can also influence animal abundance, habitat selection, or seasonal movements (e.g. Fryxel and Sinclair 1988, Illius and O´Connor 2000, Klein 1970, Mobæk et al. 2009, Pettorelli et al. 2001, Seagle and McNaughton 1992, Van Beest et al. 2010, Youngentob 2011).

From a herbivore's perspective, a high quality food item is the one containing higher levels of digestible nutrients (i.e. nitrogen and digestible energy) and lower levels of digestibility-reducing substances, such as cell wall constituents (i.e. fiber) and secondary metabolites (i.e. phenolics; e.g. Bergeron and Jodoin 1987, Berteaux et al. 1998, Robbins 1993). Nitrogen is often a limiting element to plant growth in the boreal ecoregion (Larsen 1980, Tamm 1991) and through cascade effects, may also play a key role in herbivore diet selection and nutrition (Mattson 1980), and a continuous intake of dietary nitrogen is indeed a necessity for herbivores (Mattson 1980, Robbins 1993, White 1993). Moreover, low levels of plant nitrogen are associated with higher concentrations of cell wall constituents and secondary metabolites, and therefore consumption of forage containing low levels of nitrogen results in a low nutrient intake as well as in reduced digestibility (Palo et al. 1985, Robbins 1993, Van Soest 1994). Fibrous food generally increases retention time in the digestive tract of animals and consequently reduces digestible energy intake per time unit (Van Soest 1994). Concentrations of secondary metabolites (i.e. total phenolics and condensed tannins) also influence the quality of food through their digestibility-reducing properties (Estell 2010, Iason 2005, Palo and Robbins 1991). Condensed tannins are able to bind or precipitate with plant proteins and gastrointestinal enzymes, and therefore can significantly reduce protein digestion (Palo and Robbins 1991, Spalinger et al. 2010, Zucker 1983). It has been shown that increasing concentrations of phenolic compounds in herbivore diet led to reduced voluntary food intake in studied animals (Iason and Palo 1991). However, the role of tannins in defending plants against ruminants depends upon the specific tannin characteristics as well as on the physiology of

animals, since herbivore species differ in their capability to digest tanniferous forages (Hagerman et al. 1992, Salminen and Karonen 2011).

Plants available in summer, in terms of forage for herbivores, are generally of higher quality than in winter, when plants are usually less digestible and have lower amounts of necessary nutrients and minerals (Oldemeyer et al. 1977, Van Soest 1994). During summer, the quality of plant nutrients peaks at the beginning of the growing season and successively declines throughout the growing season (Van Soest 1994, McArt et al. 2009). Although the effects of winter nutrition and related reduction in food quality has generally been considered as one of the main factors influencing populations of large herbivores (e.g. Christianson and Creel 2007, Fauchald et al. 2004, Parker et al. 2005, Wallmo et al. 1977), a growing body of literature has emphasized that foraging conditions and nutrient intake during the summer might have even larger effects on populations of large herbivores; i.e. such as positive effects of high quality summer foods on growth which can greatly influence fall body reserves of many animals and subsequently their ability to reproduce or survive (e.g. Cook et al. 2001, Crête and Huot 1993, McArt et al. 2009, Parker et al. 2009, Stewart et al. 2005, Tollefson et al. 2010, White 1983).

Plant nutrients vary in space and time both within and among plant species, at fine scales, and also across larger geographical scales: this variation might be driven by internal processes, such as plant growth, development, and reproduction, or as a response to herbivory, or to environmental factors such as site fertility and weather conditions (e.g. Bryant et al. 1983, Crawley 1997, Hartley and Jones 1997, Palo and Robbins 1991). All these sources of variation create a heterogeneous environment where herbivores have to make foraging decisions and deal with variation in food resources at different spatiotemporal scales (Bailey et al. 1996, Senft et al. 1987). It has been suggested that spatial variation in food quality at the landscape scale might allow herbivores to compensate for temporal variation caused by weather, and therefore weaken its effects by improving nutrition of individuals (Wang et al. 2006, Fryxell et al. 2005). For instance, large herbivores move to track environmentally induced variation in plant phenology in order to select new emerging plants, which are of high nutritional value, and thus prolonging access to a diet high in protein and low in digestibility-reducing compounds (Albon and Langvatn 1992, Singh et al. 2010, White 1983).

The influence of climate conditions on populations of large herbivores has attracted a great deal of interest (e.g. Anouk Simard et al. 2010, Post and Forchhammer 2008, Weladji and Holand 2003). Climatic stochasticity may act directly on the animals, for example the effect of harsh winter may lead to increased costs of thermoregulation (Parker and Robbins 1985), and increasing snow cover to increased costs of mobility and thus affect herbivore body condition (Parker et al. 1984). Climate may also act indirectly on herbivores through its effects on forage plants, resulting in temporal variation in food quality among and within seasons by altering plant phenology, concentrations of nutrients and anti-herbivore defenses of plants (Albon and Langvatn 1992, Cleland et al. 2007, Lenart et al. 2002, Post et al. 2008). Since the growth, reproduction and survival of herbivores are dependent on the

quality of eaten plants, the effects of climate changes and extreme weather conditions on forage plants might strongly alter the population dynamics of these animals (Post and Forchhammer 2001, Van der Putten et al. 2010).

Some studies have investigated variation in plant nutrients among years (e.g. Bø and Hjeljord 1991, Graglia et al. 2001, McArt et al. 2009, Riipi et al. 2004), or reported the spatial variation in plant nutritional characteristics over smaller geographical areas (e.g. Baraza et al. 2009, McArt et al. 2009, Graglia et al. 2001, Stolter et al. 2010), but in view of the importance of understanding at what scale this variation occurs, we have to evaluate spatial and temporal variation in herbivore food quality at multiple scales and to do this at the same time in the same system. Such studies of nutritional aspects of food quality over large geographical areas have also increasing importance in the face of forecasted climate changes. Nevertheless, such analyses are rare since they require enormous numbers of samples of diverse plant species and therefore frequently become so time-consuming and expensive. Near infrared reflectance spectroscopy (NIRS) provides a useful tool to overcome these drawbacks since it allows rapid and non-destructive analyses of large numbers of samples (Foley et al. 1998).

Furthermore, to efficiently investigate large scale questions like that of global change, ecologists want to know where most variation in food quality lies. For example, if an ecologist knew that variation at the local level was just 5% of that at higher levels (or among years), they might allocate their sampling very differently than if all spatiotemporal scales had similar variation. Therefore, because so little is known about spatial and temporal variation in food quality in a natural system, here I assess the spatial and temporal variation in the quality of two plant species (using NIRS) in the diet of an important herbivore in the boreal system, the moose (*Alces alces*), for three subsequent years along a latitudinal gradient spanning over 1 200 km of varying environmental conditions. The moose is of great economic importance to hunters (Mattson 1990) and affects the structure and functioning of the boreal ecosystem (Persson et al. 2000). Downy birch (*Betula pubescens* L.) and fireweed (*Epilobium angustifolium* L.) are two important plant species in moose summer diet. They were selected for this analysis due to their physiological differences (i.e. the leaves of a deciduous tree and the above-ground parts of a perennial herb), and thus may better reflect the variation within diverse diet of a herbivore, like the moose.

Specifically, I test: (i) if food quality varies with latitude for these two foods. In addition, I quantify: (ii) the temporal variation (i.e. year-to-year) in summer food quality, (iii) the degree of spatial variation in summer food quality at the local scale, and (iv) the degree of spatial variation in food quality at a much larger (regional) scale. Most importantly, because few studies have compared the relative magnitude of variation from various spatiotemporal sources that herbivore face, I do so here (v).

Materials and Methods

Sample collection and preparation

To assess how summer food quality varies over different spatiotemporal scales, samples of downy birch and fireweed were collected in five different areas along a latitudinal gradient in Sweden (Figure 1).

The northernmost study area, Råneå (66° 1´N, 21° 58´E), is situated on the edge between the middle boreal and north boreal vegetation zones. Sorsele (65° 32´N, 17° 31´E) is located in the north boreal vegetation zone. Furudal (61° 10´N, 15° 7´E) is located on the edge of the middle boreal and north-boreal vegetation zones. Malingsbo (59° 55´N, 15° 27´E) is located on the edge of the south boreal and middle boreal vegetation zones, and finally Misterhult (57° 27´N, 16° 32´E) is situated in the hemi boreal vegetation zone in south-eastern Sweden (Ahti et al. 1968). Due to the large latitudinal extent of Sweden a wide range of weather-related characteristics can be found between individual study areas (Table 1).

Figure 1: Location of study areas in Sweden.

Table 1. Weather-related characteristics of individual study areas, period 1961 - 1990 (SMHI 2012).

	Mean annual temperature (°C)	Mean annual precipitation (mm)	Length of growing season (days)	Average number of days with snow cover
Råneå	0	600	140	175
Sorsele	-2	500	130	200
Furudal	2	700	160	150
Malingsbo	4	700	170	150
Misterhult	6	500	190	75

Each birch sample represents long-shoot leaves stripped from at least 10 different randomly-selected birch trees within the range that moose can browse (i.e. 0,5 - 3m; Ball and Dahlgren 2002, Lavsund 1987) within a distance of about 100 m. In case of fireweed, at least 10 different randomly selected individual plants not growing closer to each other than 2 m were collected within a distance of about 100 m to represent one sample.

To quantify the local scale, samples were collected within the individual study areas of average size of about 400 km^2, which corresponds to a circle of a radius of 11 km. To quantify the regional scale, the study areas were in average of about 280 km apart and were spread over a north-south gradient of about 1 200 km. To quantify the temporal variation, samples were taken over three consecutive years (2008, 2009, 2010) at the end of the growing season, and care was taken to ensure that the collection of the plant samples in

individual study areas took place at the same time every year since the concentrations of plant chemical constituents vary over a growing season (Nurmi et al. 1996). Furthermore, every yearly collection started in the south and proceeded northwards to help ensure that all samples were collected at the same phenological state of plant development. Sampling dates in individual study areas and years are shown in Appendix (Table A2).

All plant samples were then placed into paper bags and oven-dried to constant weight at about 35°C as the low temperatures are thought to minimise degradation of the active components in plant tissues (Harbourne et al. 2009). The dried samples were then ground to pass 0.5 mm sieve using a Cyclotec™ 1093 Sample Mill (Tecator, Höganä, Sweden). All samples were stored in airtight plastic cups in the dark at a constant temperature.

Near infrared reflectance spectroscopy (NIRS): collection of reflectance spectra

Near infrared reflectance spectroscopy was used to assay nutrient composition (i.e. nitrogen, acid detergent fiber (ADF), total phenolics and condensed tannins) of the two plant species. NIRS is based on the development of a calibration equation that reflects the relationship between NIR spectral information and chemical constituents of samples (Foley et al. 1998). The hydrogen bonds in water absorb significant amounts of NIR radiation that may obscure other relationships in the reflectance spectrum of the sample (Abrams 1985, Foley et al. 1998), so I dried all samples in an oven at 35°C for at least 12h to remove any residual moisture and then placed them into a desiccator to cool to room temperature. Afterwards I carefully mixed all samples to make sure that each of them was thoroughly homogenized and then I packed each sample into a small ring cup with a quartz glass cover on one side and back sealed with disposable paper on the other side; care was taken to ensure that the sample was spread evenly and compressed to a consistent degree of compression (Foley et al. 1998). I recorded the reflectance spectrum of each sample with a NIRSystems model 6500 scanning spectrophotometer (FOSS NIRSystems Inc., Silver Spring, MD, USA) equipped with a spinning cup attachment. This spectrum produced by the NIRS instrument reflects the detailed chemical composition of a sample (Foley et al. 1998). The spectrum of each sample was the average of 32 successive scans and as a control, 16 scans over the standard ceramic disk were made before every sample. Each spectrum was recorded as the logarithm of the reciprocal of reflectance (log 1/R) in the wavelength range from 400 to 2500 nm at 2 nm intervals to give a total of 1050 data points per sample. I collected spectra of each sample in duplicates, and these were averaged only if the spectral noise (i.e. the root mean square of the difference between replicates) was less than 50 (Lawler et al. 2006, McIlwee et al. 2001). This ensured collection of spectral data of high precision (Shenk and Westerhaus 1993). At the beginning of each day, I performed diagnostic tests needed in order to check the accuracy of the wavelengths, and the repeatability of measurements. In order to minimise instrument variation in the measurement of spectra, the NIRS monochromator was kept in a room maintained at constant temperature and humidity. The recorded spectral data were managed using the ISIscan software, version 4.0 (Infrasoft International, State College, PA) and stored as absorbance units [A = log (1/R)].

Chemical analyses

A subset of plant samples (n = 244), further used for NIRS interpolation of chemical constituents in the remaining samples, was assayed by standard chemical methods to determine the exact concentrations of nitrogen, acid detergent fiber (ADF), total phenolics and condensed tannins. Total nitrogen content was analysed on 3-6 mg subsamples of ground plant material using a PerkinElmer 2400 CHN elemental analyzer (PerkinElmer Corp., Norwalk, Connecticut) and expressed as a percentage on a dry weight basis. The amount of ADF was determined following the methods of Goering and Van Soest (1970), modified for glass filter tubes and expressed as a percentage on a dry weight basis. This procedure extracts lignin, cellulose and cutin (i.e. compounds of low digestibility for most herbivores) and therefore provides a useful measure to compare digestibility of different plant species (Robins 1993, Van Soest 1994). Total phenolics were determined using Folin-Ciocalteu´s reagent (Singleton and Rossi 1965) with tannic acid as a standard according to method described by Waterman and Mole 1994. Absorbance of the solution was read at 760 nm and values were expressed as percentage on a dry weight basis of tannic acid equivalents. A radial diffusion method (Hagerman 1987) with an agar gel was used to measure the amount of condensed tannins and tannin content expressed as percentage (dry weight) of tannin acid equivalents.

Calibration development and prediction of chemical constituents

I used the results of the chemical assays to interpolate the concentrations of nitrogen, ADF, total phenolics and condensed tannins in the remaining birch and fireweed samples. I modelled this relationship between spectra and wet-chemistry values by modified partial least squares regression (MPLS; Shenk and Westerhaus 1991) using the spectral region between 1 100 – 2 498 nm. The MPLS approach uses cross-validation (i.e. the “leave one out method”, also known as jack-knifing) to prevent over-fitting and to select the optimum number of terms for the equation (Osborne et al. 1993). During cross-validation, one sample (i.e. the validation sample) was removed from the data set, while the remaining samples were used for calibration. This procedure was repeated for the whole dataset until each sample had been removed once. In order to reduce any possible effect of particle size variation on the NIR spectra, the scatter correction of standard normal variate (SNV) and detrend was applied to the spectral data, along with the mathematical second-order derivation of 2, 8, 6, 1 (Barnes et al. 1989, Osborne et al. 1993). The predictive ability of the MPLS equation was evaluated on the basis of coefficient of determination (R^2), standard error of cross validation (SECV; Mark and Workman 1991) and ratio performance deviation (RPD; Williams and Soberig 1992). Calibration and predictions were performed using the WinISI software, version 4.5 (Infrasoft International, State College, PA).

Statistical analyses

Descriptive statistics (i.e. mean, standard error, coefficient of variation) along with graphics were used for all variables in both plant species to summarize and describe the data collected in individual study areas and years. I used the linear mixed-effects models (LME) with the package *lme4* (Bates et al. 2012) in order to assess the relationships between species, study areas (i.e. latitude), years and nutritional quality (i.e. nitrogen, fiber, total phenolics, and condensed tannins). LME´s are useful for modelling non-independent and repeated observations (Demidenko 2004). In order to estimate spatial and temporal variation in individual nutrients in birch and fireweed along a latitudinal gradient, I split the dataset based on individual species and then formulated linear mixed models with location and year as fixed effects. In addition to these fixed effects, I also included a random year-effect into the models to account for temporal stochasticity (Pinheiro and Bates 2000). All additive models were fitted by the *lmer* function and estimated with restricted maximum likelihood (REML). To assess the validity of the models, I performed likelihood ratio tests comparing the models with fixed effects to the null models with only the random effects. Markov Chain Monte Carlo (MCMC) p-values were estimated to assess the significance levels (at $\alpha < 0.05$ level). The model selection was done using the *dredge* function from the *MuMIn* (Bartoń 2012) package and the best model was selected based on the lowest Akaike's Information Criterion (AIC) values (Burnham and Anderson 2002). The final models estimated after model averaging (using '*AICcmodavg*' package; Mazerolle 2012) are presented. To quantify the degree of spatial and temporal variation in food quality, I estimated the species-specific coefficients of variation (i.e. CV, standard error divided by mean) for concentrations of nitrogen, ADF, total phenolics, and condensed tannins at local (i.e. within individual study areas), regional (i.e. among individual study areas), and yearly scales. To determine whether there was any pattern in variation at the local scale along a latitudinal gradient, I considered both species together and calculated the non-parametric Kendall´s tau τ correlation coefficient between coefficients of variation and latitude. Finally, in order to evaluate the extent of variability in food quality experienced due to all spatiotemporal factors, I compared the species specific coefficients of variation for individual nutrients at the local, regional, and yearly scales. The results are graphically presented and CVs for each level of variation are represented by mean values. All statistical analyses were performed with the R software, version 2.14.2 (R Development Core Team, 2009).

Results

NIRS predictions

Overall, a total of 842 plant samples, including 438 downy birch samples and 404 fireweed samples was analysed for concentrations of nitrogen, ADF, total phenolics and condensed tannins. Exact numbers of birch and fireweed samples collected in individual study areas and years are shown in Appendix (Table A1). My calibration equations (derived

from the absorbance spectra of plant tissues) allowed precise estimations of all chemical constituents in the plant samples (Table 2). For most readers, the R^2 column provides the easiest way to conceptualize the performance of both the chemical analyses and the NIRS scanning of reflectance spectra. Specifically, a given sample was dropped from the model during the cross validation procedure, and the value of that particular nutrient for that sample was predicted by NIRS; the high R^2 values in Table 2 suggest a very high degree of precision in both of the two independent steps of chemical analysis and NIRS scanning.

Table 2. Predictive power of modified partial least square regression with cross-validation (jackknifing) for modeling the relationship between spectral characteristics of plant samples and concentrations of nitrogen, ADF, total phenolics and condensed tannins.

Constituent	**N**	**SD**	**Bias**	**Slope**	**R^2**	**SEP**	**RPD**
Nitrogen	87	0.526	-0.002	0.999	0.99	0.04	13.15
ADF	174	9.319	0.003	1.003	0.93	2.38	3.92
Total phenolics	176	2.306	-0.007	0.999	0.95	0.51	4.52
Condensed tannins	170	2.041	0.005	1.005	0.97	0.32	6.38

N=the number of samples used for calibration; SD=standard deviation of laboratory reference values; R^2=the degree of correlation between the predicted values and the actual measured values; SEP=standard error of prediction; RPD=SD/SEP-ratio performance deviation; RPD > 3 indicates good models (Williams 2001).

Nutrient characteristics of birch and fireweed

The concentrations of nutrients differed between the two plant species (Table 3). Downy birch had much higher concentrations of ADF and slightly higher concentrations of nitrogen in comparison to fireweed. The content of total phenolics and condensed tannins was greater in fireweed than in birch. All chemical constituents showed larger variation in fireweed than in birch. ADF was the least variable compound in both plant species (5% for birch, 10% for fireweed). Condensed tannins had the highest CV (17%) compared to the rest of the constituents in birch. In case of fireweed, nitrogen was the most variable compound (22%), following by total phenolics (21%) and condensed tannins (20%).

Table 3. Mean, standard error (SE), minimum (Min), maximum (Max) and coefficient of variation (CV) for all chemical constituents in both plant species.

	Birch					**Fireweed**				
Constituent	N	Mean ± SE	Min	Max	CV(%)	N	Mean ± SE	Min	Max	CV(%)
Nitrogen	438	1.95 ± 0.01	1.37	2.89	12	404	1.50 ± 0.02	0.76	2.88	22
ADF	438	59.72 ± 0.14	50.70	67.34	5	404	45.00 ± 0.22	33.97	61.63	10
Total phenolics	438	11.58 ± 0.07	5.97	14.79	13	404	12.68 ± 0.13	3.24	20.30	21
Condensed tannins	438	2.48 ± 0.02	1.13	3.87	17	404	6.65 ± 0.07	2.28	9.85	20

All values expressed as % dry matter.

Spatial and temporal variation in food quality along a latitudinal gradient

The results of the final mixed effects models selected after model selection and averaging are shown in Table 4 (for downy birch) and Table 5 (for fireweed). The final models showed that location had a significant effect on the concentrations of all chemical constituents in both plant species. The effect of individual years was not significant for any of the response variable, however after model selection and averaging, year was retained in all final models.

Table 4. Coefficient estimates, standard error estimates (SE), and p-values for the predictors of all response variables in the final linear mixed model for downy birch (*Betula pubescens*).

	Nitrogen		**ADF**		**Total phenolics**		**Condensed tannins**	
	Estimate ± SE	pMCMC	Estimate ± SE	pMCMC	Estimate ± SE	pMCMC	Estimate ± SE	pMCMC
Intercept	1.87 ± 0.04	**0.0001**	55.92 ± 0.42	**0.0001**	10.86 ± 0.26	**0.0002**	2.16 ± 0.07	**0.0004**
Sorsele	0.22 ± 0.03	**0.0001**	3.41 ± 0.34	**0.0001**	0.06 ± 0.21	0.7750	0.04 ± 0.06	0.5146
Furudal	0.07 ± 0.03	**0.0370**	0.99 ± 0.34	**0.0024**	0.34 ± 0.21	0.1056	0.16 ± 0.06	**0.0060**
Malingsbo	0.11 ± 0.03	**0.0010**	2.19 ± 0.34	**0.0001**	0.49 ± 0.21	**0.0222**	0.24 ± 0.06	**0.0001**
Misterhult	0.26 ± 0.03	**0.0001**	3.74 ± 0.34	**0.0001**	-0.83 ± 0.22	**0.0002**	0.05 ± 0.06	0.4000
Year (2009)	-0.02 ± 0.05	0.8012	1.84 ± 0.50	0.3252	1.05 ± 0.32	0.3480	0.38 ± 0.09	0.2828
Year (2010)	-0.10 ± 0.05	0.5096	3.29 ± 0.50	0.1858	1.00 ± 0.32	0.3542	0.28 ± 0.09	0.3610

p-values are based on Markov Chain Monte Carlo simulations. Råneå and year (2008) represent the base.

Table 5. Coefficient estimates, standard error estimates (SE), and p-values for the predictors of all response variables in the final linear mixed model for fireweed (*Epilobium angustifolium*).

	Nitrogen		**ADF**		**Total phenolics**		**Condensed tannins**	
	Estimate ± SE	pMCMC	Estimate ± SE	pMCMC	Estimate ± SE	pMCMC	Estimate ± SE	pMCMC
Intercept	1.25 ± 0.05	**0.0018**	43.73 ± 0.65	**0.0001**	13.33 ± 0.31	**0.0001**	7.14 ± 0.17	**0.0001**
Sorsele	0.19 ± 0.04	**0.0001**	-1.15 ± 0.51	**0.0220**	0.60 ± 0.25	**0.0150**	0.08 ± 0.13	0.5484
Furudal	0.25 ± 0.04	**0.0001**	0.41 ± 0.52	0.4376	-1.09 ± 0.25	**0.0001**	-0.67 ± 0.13	**0.0001**
Malingsbo	0.37 ± 0.04	**0.0001**	1.25 ± 0.52	**0.0210**	-1.70 ± 0.25	**0.0001**	-0.88 ± 0.14	**0.0001**
Misterhult	0.59 ± 0.04	**0.0001**	7.74 ± 0.59	**0.0001**	-5.27 ± 0.29	**0.0001**	-2.63 ± 0.15	**0.0001**
Year (2009)	-0.11 ± 0.06	0.4588	1.94 ± 0.80	0.3882	-0.59 ± 0.39	0.5618	-0.42 ± 0.21	0.4630
Year (2010)	0.09 ± 0.06	0.5240	-1.36 ± 0.80	0.5120	1.92 ± 0.38	0.2260	0.87 ± 0.21	0.2736

p-values are based on Markov Chain Monte Carlo simulations. Råneå and year (2008) represent the base.

Focusing on variation in nutrient composition in birch (Table 4), the results of the final model showed that among individual study areas, birch had the lowest contents of nitrogen in Råneå (indicated by positive coefficient estimates for all other areas), whereas the highest levels of nitrogen were in Misterhult (0.26 ± 0.03, $p < 0.0001$), followed by Sorsele (0.22 ± 0.03, $p < 0.0001$), Malingsbo (0.11 ± 0.03, $p < 0.0001$), and Furudal (0.07 ± 0.03, $p < 0.0370$). The effect of year was not significant, but amount of nitrogen in birch was slightly lower in both 2009 and 2010 compared to 2008 (Figure 2).

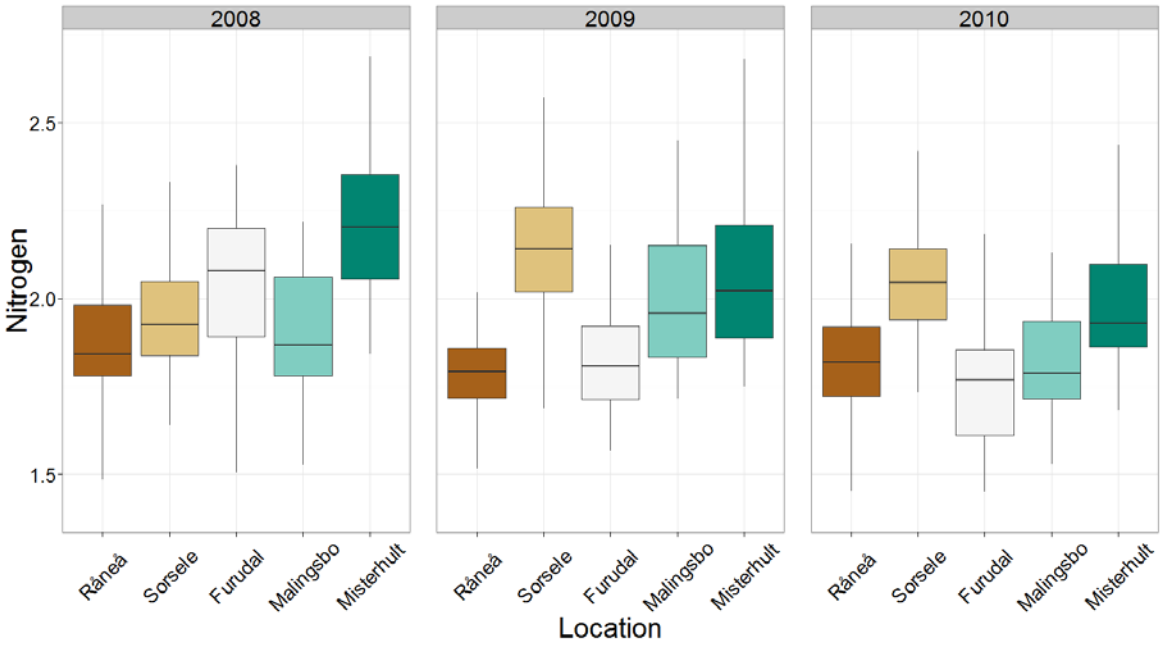

Figure 2. Box and whisker plots showing the median, minimum, maximum, upper and lower quartile for the concentrations of nitrogen in downy birch (*Betula pubescens*) in individual study areas and years (the latitudinal gradient runs from Råneå in the north to Misterhult in the south).

The concentrations of ADF showed similar trends among individual study areas as nitrogen (Table 4). The effect of the year on the concentrations of ADF was not significant, however differed in comparison to nitrogen. In both 2009 and 2010 birch had higher ADF levels than in 2008 (Figure 3).

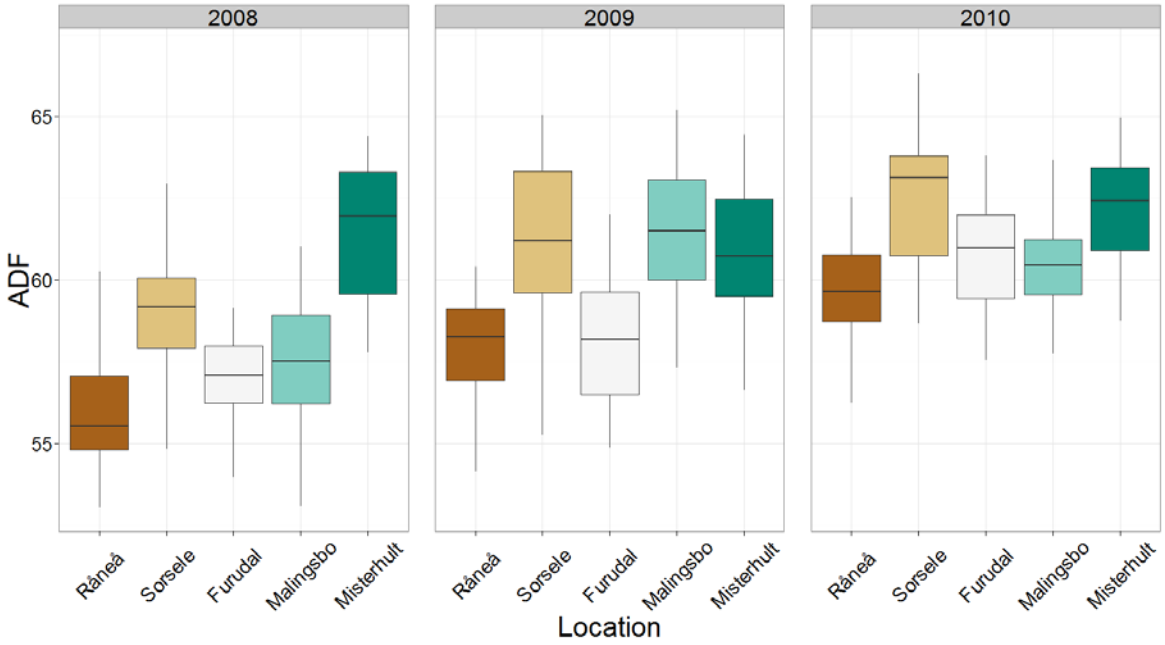

Figure 3. Box and whisker plots showing the median, minimum, maximum, upper and lower quartile for the concentrations of ADF in downy birch (*Betula pubescens*) in individual study areas and years (the latitudinal gradient runs from Råneå in the north to Misterhult in the south).

Total phenolics showed different trends among individual study areas in comparison to nitrogen and ADF. The amount of total phenolics in birch was highest in Malingsbo (0.49 ± 0.21, $p < 0.0222$), following by Furudal (0.34 ± 0.21, $p < 0.1056$), Sorsele (0.06 ± 0.21, $p < 0.7750$) and Råneå. However, the concentrations of total phenolics in Furudal and Sorsele were not significantly different than in Råneå. Misterhult had the lowest levels of total phenolics among the study areas (-0.83 ± 0.22, $p < 0.0002$). The differences in total phenolics between individual years were not significant, but total phenolics were lower in 2008 than in both 2009 and 2010 (Figure 4).

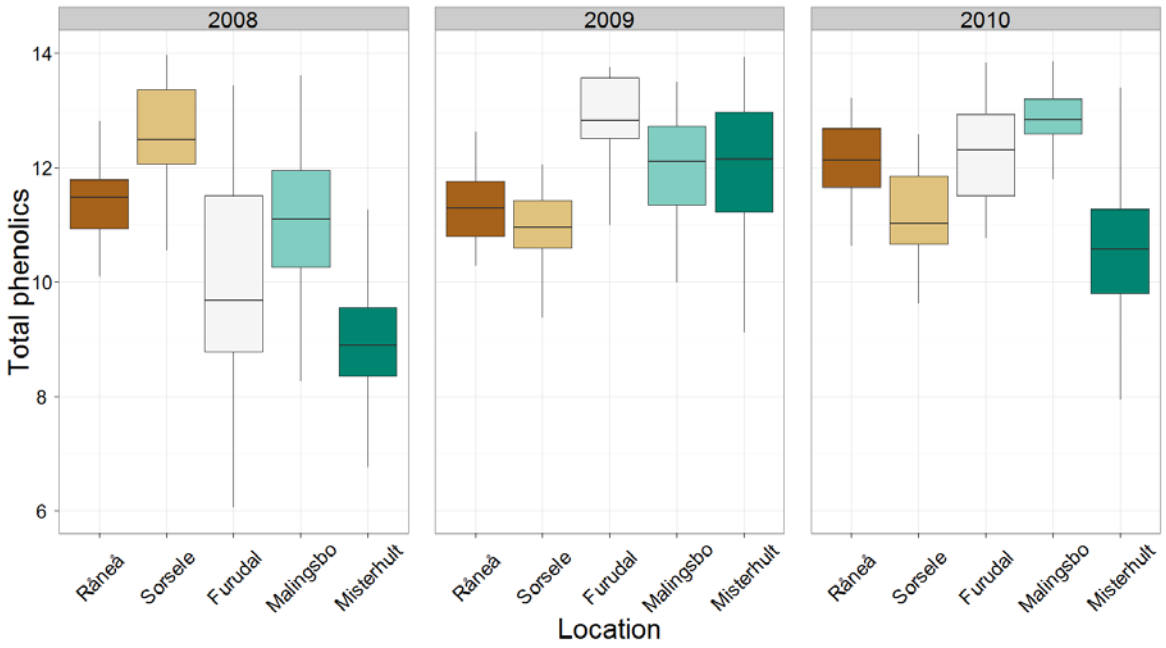

Figure 4. Box and whisker plots showing the median, minimum, maximum, upper and lower quartile for the concentrations of total phenolics in downy birch (*Betula pubescens*) in individual study areas and years (the latitudinal gradient runs from Råneå in the north to Misterhult in the south).

Concentrations of condensed tannins in birch were highest in Malingsbo (0.24 ± 0.06, $p < 0.0001$), following by Furudal (0.16 ± 0.06, $p < 0.0060$), Misterhult (0.05 ± 0.06, $p < 0.4000$), and Sorsele (0.04 ± 0.06, $p < 0.5146$), but Misterhult and Sorsele were not significantly different than Råneå. The effect of year on the concentrations of condensed tannins was the same as in case of total phenolics, with the lowest tannin contents in 2008 (Figure 5).

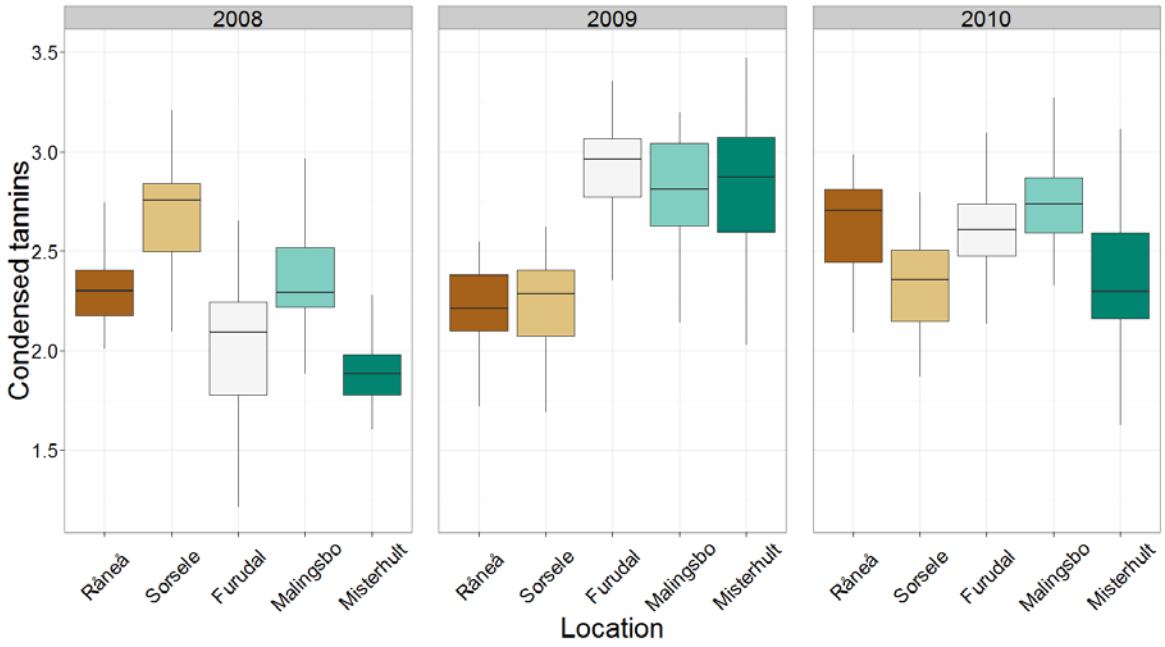

Figure 5. Box and whisker plots showing the median, minimum, maximum, upper and lower quartile for the concentrations of condensed tannins in downy birch (*Betula pubescens*) in individual study areas and years (the latitudinal gradient runs from Råneå in the north to Misterhult in the south).

Turning now to nutrient concentrations in fireweed (Table 5), the amounts of nitrogen were lowest in Råneå, whereas highest in Misterhult (0.59 ± 0.04, $p < 0.0001$), followed by Malingsbo (0.37 ± 0.04, $p < 0.0001$), Furudal (0.25 ± 0.04, $p < 0.0001$), and Sorsele (0.19 ± 0.04, $p < 0.0001$). Again the effect of year was not significant, but the contents of nitrogen were lower in 2009 than in both 2008 and 2010 (Figure 6).

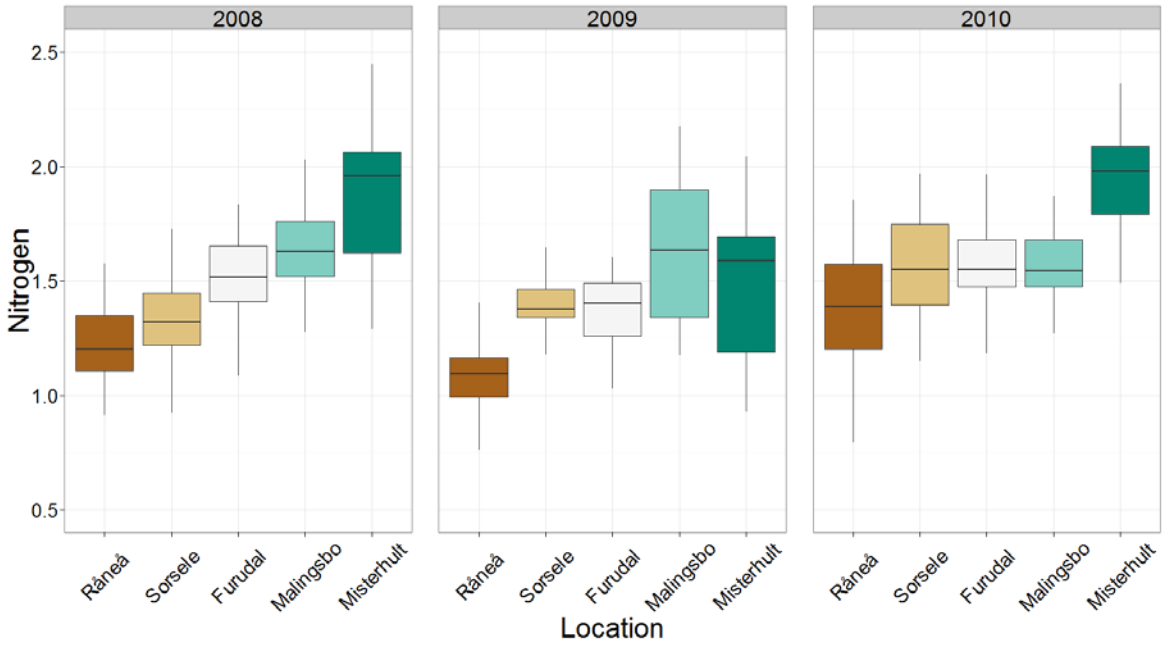

Figure 6. Box and whisker plots showing the median, minimum, maximum, upper and lower quartile for the concentrations of nitrogen in fireweed (*Epilobium angustifolium*) in individual study areas and years (the latitudinal gradient runs from Råneå in the north to Misterhult in the south).

ADF in fireweed showed a similar trend as nitrogen (Table 5), except Sorsele (-1.15 ± 0.51, $p < 0.0220$), where the levels of ADF were lower than in Råneå and the amounts of ADF in Furudal were not significantly different compared to Råneå ($p < 0.4376$). The effect of year was again not significant, but showed a different trend than nitrogen. The levels of ADF were higher in 2009 than in both 2008 and 2010 (Figure 7).

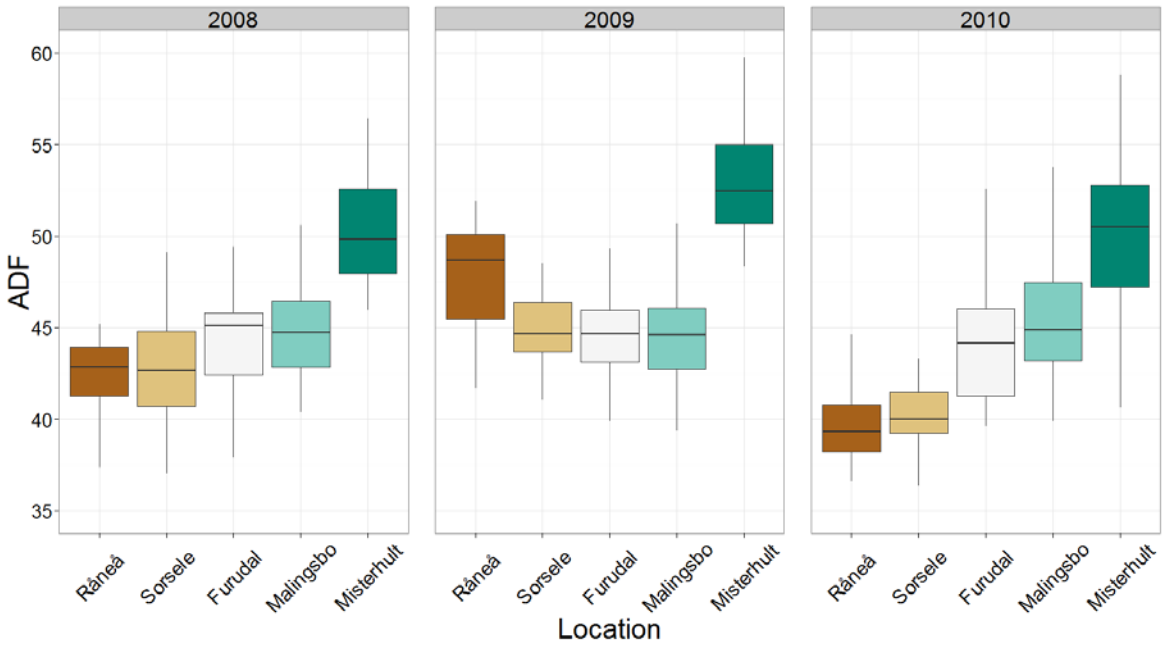

Figure 7. Box and whisker plots showing the median, minimum, maximum, upper and lower quartile for the concentrations of ADF in fireweed (*Epilobium angustifolium*) in individual study areas and years (the latitudinal gradient runs from Råneå in the north to Misterhult in the south).

Concentrations of total phenolics in fireweed showed a different trend to ADF and nitrogen. The highest amounts of total phenolics were in Sorsele (0.60 ± 0.25, $p < 0.0150$), but not significantly different from Råneå. The levels of total phenolics were the lowest in Misterhult (-5.27 ± 0.29, $p < 0.0001$), and both Furudal (-1.09 ± 0.25, $p < 0.0001$) as well as Malingsbo (-1.70 ± 0.25, $p < 0.0001$) had lower concentrations of total phenolics than Råneå. The effect of year was not significant, but amount of total phenolics was lower in 2009 compared to 2008 and 2010 (Figure 8).

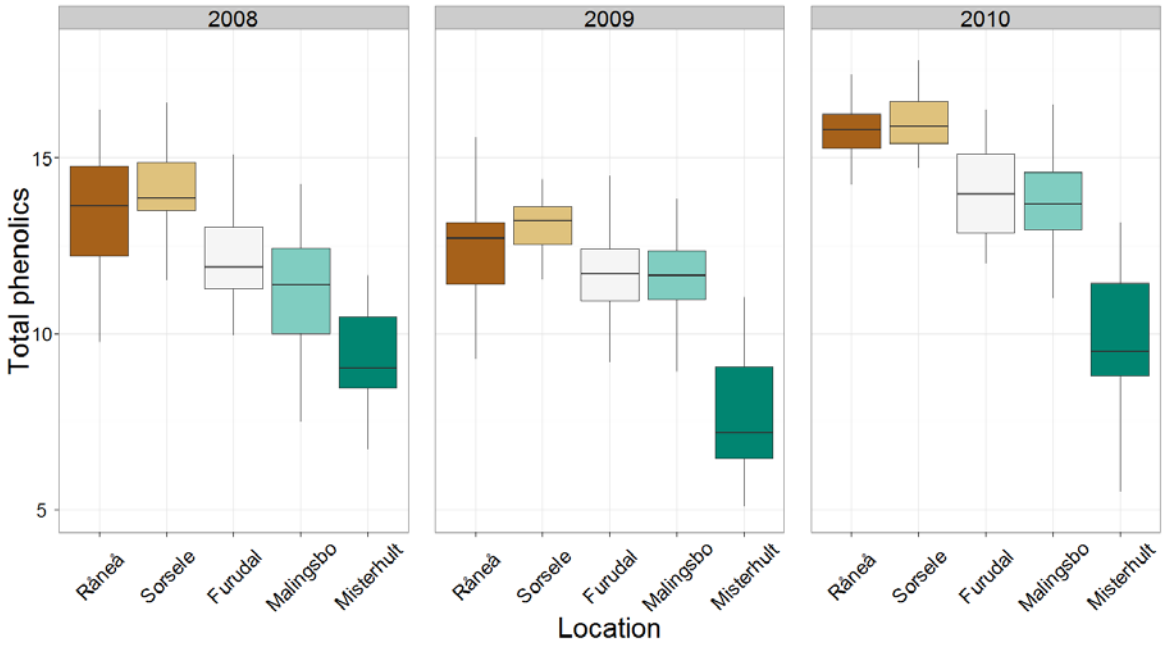

Figure 8. Box and whisker plots showing the median, minimum, maximum, upper and lower quartile for the concentrations of total phenolics in fireweed (*Epilobium angustifolium*) in individual study areas and years (the latitudinal gradient runs from Råneå in the north to Misterhult in the south).

The trends in total phenolics in fireweed were also echoed for condensed tannins (Table 5), but levels of tannins in Sorsele were not significantly different than in Råneå ($p < 0.5484$; Figure 9).

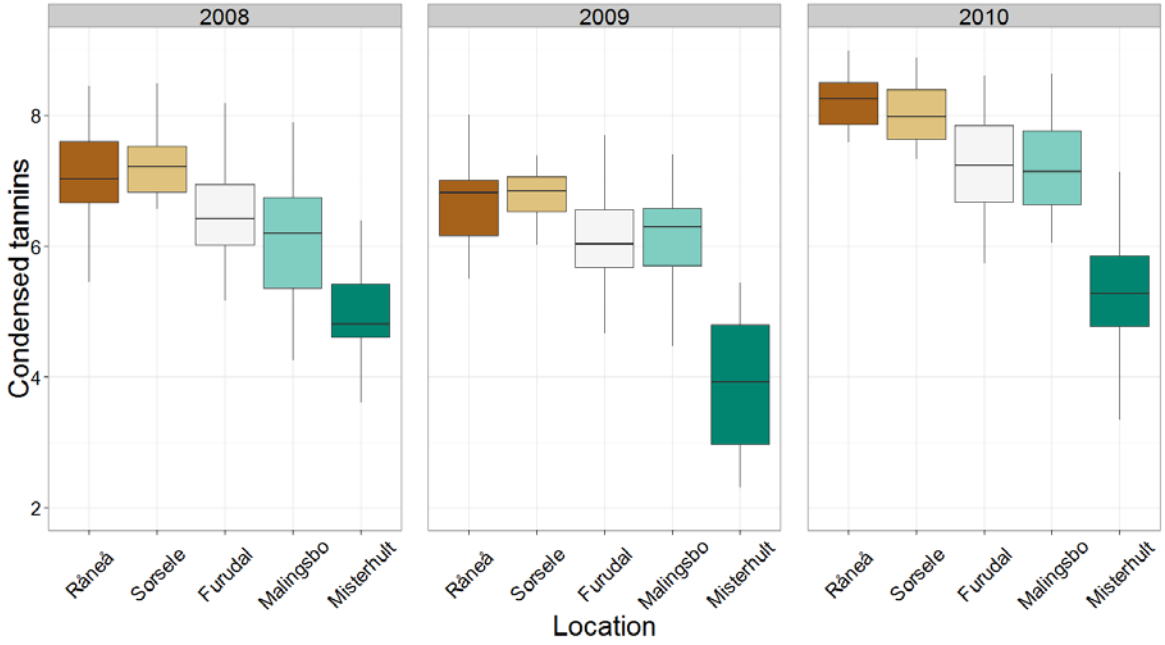

Figure 9. Box and whisker plots showing the median, minimum, maximum, upper and lower quartile for the concentrations of condensed tannins in fireweed (*Epilobium angustifolium*) in individual study areas and years (the latitudinal gradient runs from Råneå in the north to Misterhult in the south).

The latitude effect on nutrient concentrations

There was a clear latitudinal pattern in both nitrogen and ADF, both significantly increasing with decreasing latitude in both plant species, whereas trends in total phenolics and condensed tannins differed between the two plant species. Total phenolics and condensed tannins in fireweed showed clear increasing pattern with increasing latitude, but the levels of total phenolics and condensed tannins in birch did not show any pattern along a latitudinal gradient (see Figure 1 for locations).

Is there a latitudinal gradient in the variation (CVs) of nutrients?

The Kendall's tau τ correlation coefficient showed significant negative relationships between latitude and variation in total phenolics ($\tau = -0.612$, $p < 0.01$), as well as variation in condensed tannins ($\tau = -0.471$, $p < 0.05$). The relationship between latitude and variation in nitrogen ($\tau = -0.047$, $p < 0.10$), as well as variation in ADF ($\tau = 0.179$, $p < 0.10$) was not significant.

Comparing the three levels: Local, regional, and temporal variation in food quality

Considering all sources of spatiotemporal variation in nutritional aspects of food quality in both plant species, there were rather similar amounts of variation at all three spatiotemporal levels (i.e. local, regional, temporal) for all four nutritional aspect of food quality (Figures 10 to 13).

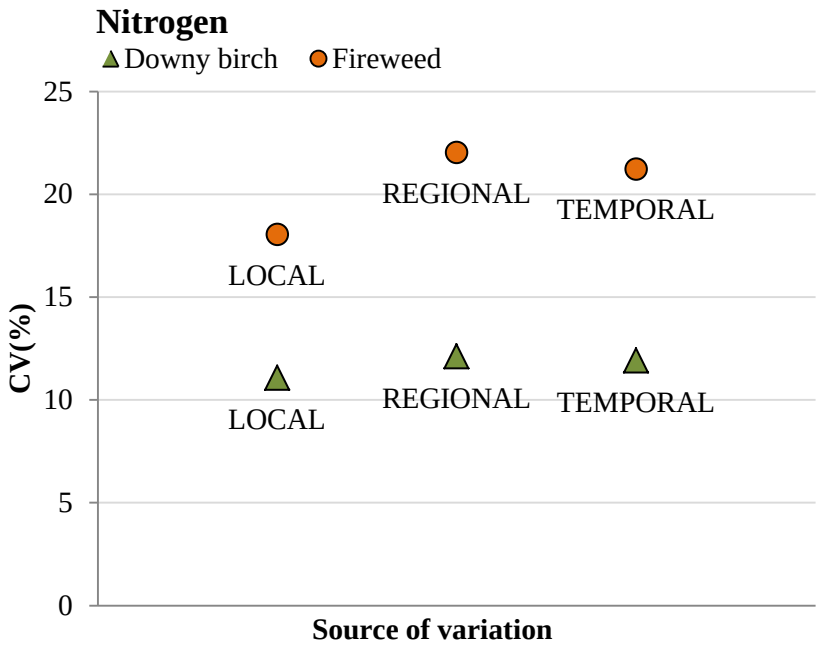

Figure 10. Variation in nitrogen at the local, regional, and temporal scale for downy birch (*Betula pubescens*) and fireweed (*Epilobium angustifolium*).

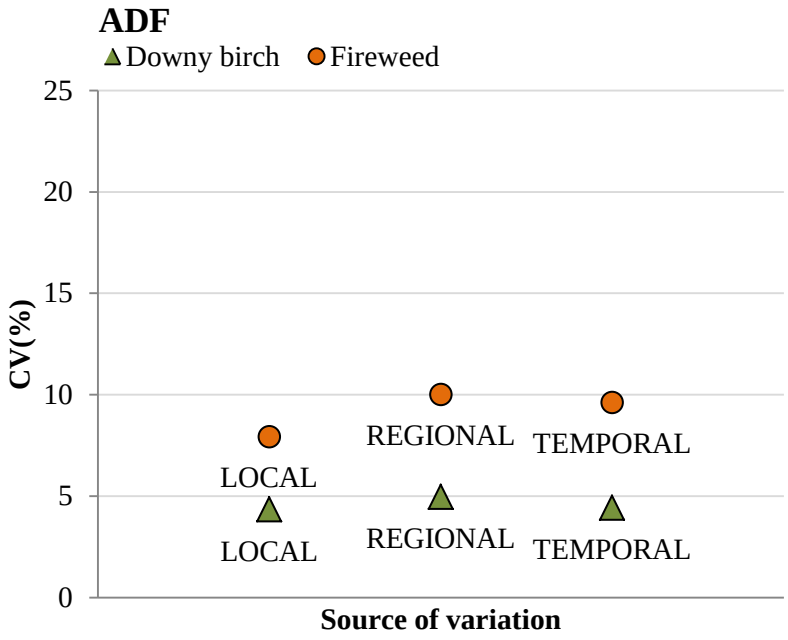

Figure 11. Variation in fiber at the local, regional, and temporal scale for downy birch (*Betula pubescens*) and fireweed (*Epilobium angustifolium*).

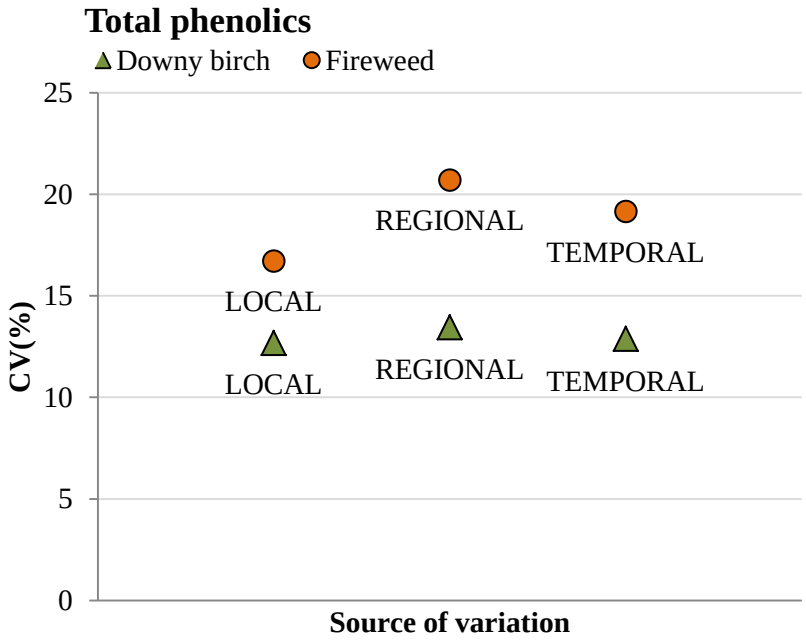

Figure 12. Variation in total phenolics at the local, regional, and temporal scale for downy birch (*Betula pubescens*) and fireweed (*Epilobium angustifolium*).

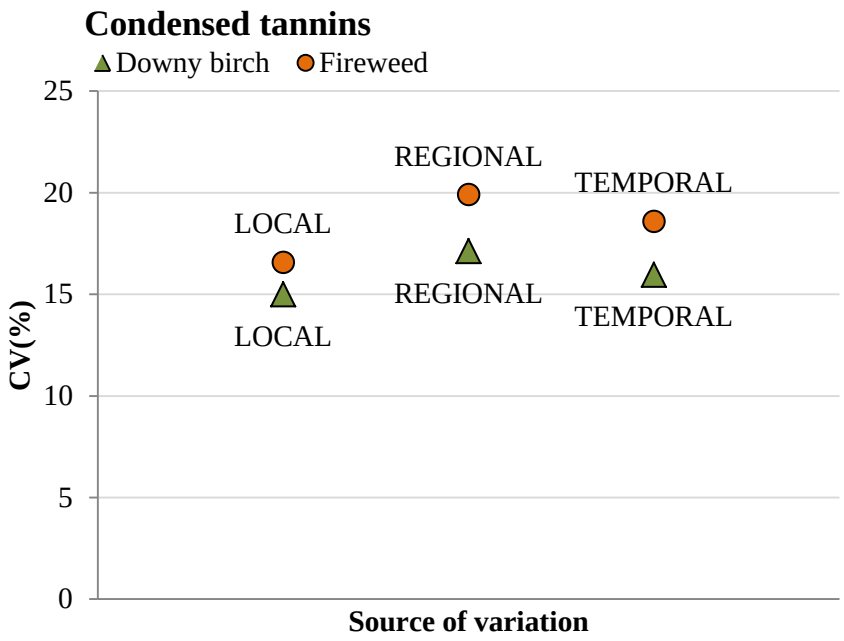

Figure 13. Variation in condensed tannins at the local, regional, and temporal scale for downy birch (*Betula pubescens*) and fireweed (*Epilobium angustifolium*).

Discussion

My analysis revealed that the degree of variation in nutritional aspects of food quality for herbivores (i.e. nitrogen, fiber, total phenolics and condensed tannins) was similar at the local level, regional level and across years. In addition, there was a clear latitudinal gradient in the concentrations of these nutrients across Sweden, where some increased and some decreased with latitude depending upon the forage species. This pattern was strongest for fireweed.

Nutritional aspects of food quality of birch and fireweed

Comparing the two study species, there was a clear difference in nutrient concentrations between downy birch and fireweed. Birch had lower levels of secondary defence compounds than fireweed, but also more nitrogen and more fiber. These differences are not surprising since I analysed the leaves of birch (a deciduous tree) and all above-ground parts of fireweed (a perennial herb). These plants differ in their life history traits, extent of root system, and nutrient demands, which contributes to differences in their nutritional characteristics. Possibly because of the fast growth rate of fireweed, the variation of all nutrients was higher than in birch.

Generally, digestibility is positively correlated with the concentrations of nitrogen and negatively correlated with the levels of fiber and secondary metabolites (i.e. phenolics,

tannins; e.g. Forsyth et al. 2005, Mattson 1980, Palo and Robbins 1991, Tahvanainen et al. 1991). Ball et al. (2000) reported that moose and other herbivores preferred to browse experimentally-fertilized pines which were higher in nitrogen concentrations than controls (i.e. 1.6% vs. 1.0% N), suggesting the importance of nitrogen in the foraging choices made by herbivores. Other studies indicate that herbivores select their food in order to reduce intake of secondary defence compounds and that nitrogen may be of lesser importance in the foraging decisions (e.g. Shipley et al. 1998, Stolter et al. 2005). Dostaler et al. (2011) showed that animal preferences for nitrogen-rich plants were dependent on the period of food selection, and Oftedal (1991) proposed that nitrogen may not be a limiting element for animals under some conditions. Thus, many factors are involved in herbivore food choices and some herbivores consume a diversity of plant species in order to balance their nutrient demands (Palo and Robbins 1991) and avoid saturating any particular detoxication pathway (Stolter et al. 2005).

Spatial and temporal variation in food quality along a latitudinal gradient

The latitudinal trends my analysis revealed probably reflect a gradient of climatic conditions that vary from milder in the south to increasingly harsh in the north. The longer period with snow cover, the length of the growing season, or other factors like temperature and precipitation (Table 1) contribute to the spatiotemporal dynamics of plant nutrients (Mårell 2006). The implications of these differences in growing season lengths and other environmental factors are reflected in the life history of plants occurring throughout this gradient, whereby certain plant species at northern latitudes achieve higher quality over shorter periods of time compared to those at southern and milder areas (Bliss 1962). Hence, the species in the north, even though existing in harsher conditions, may not necessarily be of lower quality, although this may vary with species (Chapin 1987, Klein 1970). In addition, the length of the growing season interacts with other environmental factors, such as local climatic conditions, soil water content, and soil nutrient availability (Chapin 1987). For different kinds of plants, the patterns of variation in nutrient concentrations substantially differ in relation to these environmental factors (Reich and Oleksyn 2004). My analysis, for instance, revealed that both birch and fireweed showed an increase in nitrogen and fiber content from north to south, whereas the concentrations of total phenolics and condensed tannins in fireweed showed the opposite. Moreover, total phenolics and condensed tannins in birch did not show any trend with latitude in my results. The increasing trend for nitrogen towards the south which I found is consistent with Reich and Oleksyn (2004), who reported that leaf nitrogen content in both herbs and deciduous trees increases with mean annual temperature over large geographical areas. My analysis revealed the opposite latitudinal trend for nitrogen and secondary defense compounds (i.e. lower phenolics and tannins in the south), which is in agreement with the carbon-nutrient balance hypothesis (Bryant et al. 1983). This hypothesis predicts that plants growing in environments where nitrogen is limited will invest more into carbon-based compounds (i.e. phenolics and tannins), because growth is restricted, whereas plants growing in environments with higher nitrogen availability, will invest more into growth and spend less

on defense. Overall, the latitudinal trends which my study revealed suggest the importance of local climatic conditions and site fertility on the food quality for herbivores.

In addition, the climatic conditions and topography may vary to produce variability in the nutrient contents of plant species through space and time (e.g. Crawley 1983, Hartley and Jones 1997). Heterogeneous landscapes increase the ability of mammalian herbivores to access highly nutritious plants (Searle et al. 2010). Spatial variation in food quality at a regional scale might be of particular importance to large herbivores, because it may allow them to prolong the period when they can forage on highly nutritious immature plants (Albon and Langvatn 1992, Bliss 1962). Moreover, considering the differences in the length of the growing seasons (the southernmost study area has about a 50 day longer growing season, Table 1), so perhaps there is an increased potential for more variation in weather during this longer growing season. Therefore, one might expect higher nutrient variability with decreasing latitude (i.e. with increasing length of the growing season). Indeed, my analysis revealed that two of four aspects of plant quality (total phenolics, and condensed tannins) were more variable in the south where the growing seasons are longer. However, variation in nitrogen and fiber did not show any trend with latitude. Future studies should focus on mechanisms underlying these patterns. Most importantly, my analysis revealed that the nutrient variation showed to be of similar importance for all three sources of variation (i.e. local, regional and temporal). This finding suggests that ecologists working on this system in the future should not focus on any one of these three sources of variation, but may need to consider all three levels to understand herbivore foraging. Furthermore, the process of foraging decisions made by herbivores continues to yet finer scales than considered here. Significant variation in nutrients has been observed not only among individual plants, but also among individual parts of the same plant (Nordengren et al. 2003, Palo et al. 1992, Suomela and Ayres 1994). Consequently, foraging decisions begin at the regional scale, progressively getting to a finer scale through the plant community, individual plants, and finally to a plant part at the bite scale (Senft et al. 1987). I did not consider the finer scales in this study since several plants were pooled to represent one sample. My data spanned three years of sampling at both the local and regional levels-it would be very interesting to see how the relative amounts of variation might change with sampling over more years, or a higher sampling intensity.

It is worth mentioning that the latitudinal gradient in Scandinavia is already known to produce interesting patterns in structure and functioning of the boreal ecosystem and its components. For instance, the date of calving and ovulation patterns of moose vary across latitudes, body mass and life history of moose varies across the latitudinal gradient, there are patterns in calving site selection and habitat use, there are migration patterns of moose which show a clear gradient (e.g. Ericsson et al. 2002, Garel et al. 2009, Haydn 2012, Lundmark 2008, Singh et al. 2012). These patterns are likely to be influenced by factors such as food quality shown in this study, since food is one of the key determinants of life history, demography, population dynamics and hence fitness of animals (e.g. Giesel 1976, Parker et al. 2009, Pettorelli et al. 2003, McArt et al. 2009). Therefore, my results may help

further studies to relate these observed patterns and explore further relationships in the boreal system.

I did not evaluate other aspects of herbivore food quality, such as the concentrations of minerals, carbohydrates, or terpenes, since many previous studies indicate that information about nitrogen, fiber, total phenolics and condensed tannins is sufficient to capture the most important information regarding the food quality for herbivores (Albon and Langvatn 1992, Palo and Robbins 1991, Robbins 1993, Van Soest 1994). Nevertheless, even total measurements of the chemical concentrations may not perfectly reflect digestion of that food by a given herbivore. For instance, *in situ* or *in vitro* analyses of digestion of components of food quality may give us a better picture about how food quality affects animals than measurements of the total concentrations. However, such analyses are expensive and time-consuming, especially when it comes to analyses of large numbers of samples, and that is why I was not able to use such methods (nor I am aware of any studies of a similar scale to mine which used these methods). Moreover, total measures of plant secondary metabolites, such as total phenolics, do not take into account effects of specific phenolic compounds (i.e. flavonoids and phenolic glycosides) on digestibility (Stolter et al. 2005). Similarly, measures of total nitrogen ignore the fact that tannins can significantly reduce the amount of total nitrogen and thus some of this nitrogen may not be digestible for animals (Robbins 1993). Nevertheless, some mammalian species (e.g. moose) produce tannin-binding salivary proteins that may prevent tannins in browsers from reducing protein digestibility (Hagerman et al. 1992).

To conclude, my analysis suggests that in this system no single one of the three sources of spatiotemporal variation (i.e. the local, regional, and across years) in herbivore food quality dominated; all three levels were approximately of equal importance. This finding suggests that future studies must be careful to consider all the sources of variation in nutritional aspects of food quality for herbivores. In addition, there was a clear latitudinal gradient in the individual compounds of food quality, where some showed clear increasing/decreasing pattern with latitude. Further studies now can relate these observed patterns and evaluate further interactions between food quality and population dynamics of wild herbivores in the boreal system and their effects on ecosystem structure and function. My analysis also confirmed the high potential of near infrared reflectance spectroscopy (NIRS) for analysing large numbers of samples necessary for monitoring purposes over large geographical areas. The need for studies of spatiotemporal variation in the herbivore food quality over large geographical areas has increasing importance in the face of forecasted climate changes. Since the concentrations of plant nutrients and secondary defence compounds are linked to climatic variables such as temperature, precipitation, and snow cover as well as to atmospheric concentrations of carbon dioxide and ozone, the forecasted climate changes may therefore lead to significant changes of nutritional aspects of food quality for herbivores.

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Appendix

Table A1. Number of birch and fireweed samples collected in individual study areas in 2008, 2009, and 2010.

	Downy birch			Fireweed		
Study area	2008	2009	2010	2008	2009	2010
Råneå	28	30	31	29	29	31
Sorsele	30	30	30	30	30	30
Furudal	27	31	30	28	30	28
Malingsbo	30	30	28	27	25	32
Misterhult	24	29	30	15	14	26
Total	139	150	149	129	128	147

Table A2. Date of sample collection in individual study areas and years.

	Råneå	**Sorsele**	**Furudal**	**Malingsbo**	**Misterhult**
2008	Aug 2-5	July 31-Aug 1	July 12-13	July 10-12	July 7-8
2009	Aug 5-7	July 31-Aug 1	July 16	July 14-15	July 9-11
2010	Aug 5-6	Aug 1-2	July 16	July 14-15	July 9-11

SENASTE UTGIVNA NUMMER

2011:2 Vilka faktorer samvarierar med användandet av viltkött, vildfångad fisk, bär och svamp i svenska hushåll? – Stad vs. Landsbygd.
Författare: Jerker Hellstadius

2011:3 Konsekvenser av födoval och minskande sorkstammar för populationer av sorkätande ugglor och rovfåglar.
Författare: Katie Andrle

2011:4 Tjäderns (*Tetrao urogallus* L.) vinterdiet i norra Sverige: Är gran (*Picea abies*) viktig i vissa habitat?
Författare: Staffan Öberg

2011:5 Grey-sided vole and bank vole abundance in old-growth forest patches of different size and connectivity.
Författare: Niklas Paulsson

2011:6 *De novo* sequencing and SNP discovery in the Scandinavian brown bear (*Ursus arctos*).
Författare: Anita J Norman

2011:7 A genetic approach to identify raccoon dog within a large native meso-carnivore community.
Författare: Dan Wang

2011:8 Is old forest like old forest? Patterns in abundance and species number of resident birds in old boreal forest stands in relation to stand structure and landscape context.
Författare: Ortrud Leibinger

2011:9 Klövviltets nyttjande av foderraps på viltåker och betespåverkan på angränsande skog.
Författare: Maria Lidberg

2012:1 Attityder till återintroduktion av visent i Sverige
Författare: Axel Bergsten

2012:2 Viltanpassad röjning längs skogsbilvägar som en foderskapande åtgärd för älgen.
Författare: Ida Forslund

2012:3 Spawning site selection of brown trout in habitat restored streams.
Författare: Jonas Svensson

2012:4 The shift in forest and tree limits in Troms County – with a main focus on temperature and herbivores.
Författare: Kristoffer Normark

2012:5 Clover (*Trifolium* spp) gamefields: Forage product ion, utilization by ungulates and browsing on adjacent forest.
Författare: Karl Komstedt

2012:6 Habitat use and ranging behaviour of GPS tracked juvenile golden eagles *(Aquila chrysaetos)*
Författare: Carolin Sandgren